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Modeling the behavior of the northern anchovy, *Engraulis mordax*, as a schooling predator exploiting patchy prey

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Abstract—Extensive data sets on the bioenergetics of the northern anchovy, *Engraulis mordax*, and the patchy food distribution in its natural habitat allow its foraging dynamics to be inferred by modeling using techniques from population biology and behavioral ecology. The behavioral model consistently predicts that *E. mordax* grows much more slowly than would be expected with a pure, net-energy intake rate maximization strategy. The reduced growth rates could result from the fish avoiding zooplankton patches, where they are under increased predation risk, by swimming slowly in the waters between zooplankton patches. The combinations of growth rates and daily instantaneous mortality rates generated by the behavioral model are internally consistent with a Lefkovitch matrix population model, which includes an early juvenile stage of a stable and stationary population. Several novel and testable predictions are made by the behavioral model, including: (1) anchovies swim very slowly between zooplankton patch encounters; (2) within a patch fish swim very rapidly while searching for prey; and (3) fish often leave zooplankton patches before totally filling their stomachs. Given these encouraging initial results, the behavioral modeling approach appears to be a valuable technique for examining how potential habitat changes due to global warming may affect fish behavior and populations. Several such scenarios are proposed and discussed.

INTRODUCTION

THE schooling fishes of the world's oceans provide vitally needed food and important economic benefits for growing human populations. As such, any disturbances of existing species' distribution patterns or availability for harvesting may have profound consequences. One such species is the northern anchovy (*Engraulis mordax*) upon which a valuable commercial fishery is based. It has been shown that environmental changes can have both significant and unpredicted effects on *E. mordax* populations. BUTLER (1989) found that the colossal ENSO (El Niño–Southern Oscillation) event in 1982–1984 profoundly affected the growth rate of juvenile northern anchovy while effects on larval growth rate were minimal relative to the non-El Niño year of 1980. A serious concern, therefore, is that global warming will have dire long-term effects on *E. mordax* popu-

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lations. However, before we can predict the future, there must exist some level of confidence that present-day dynamics of *E. mordax* are understood. Such a task may best be accomplished by approaching problems from multiple levels: combining how populations are affected by environmental factors, and how these population-level phenomena arise from the bioenergetics and the behavior of individual fish. To this end, we use a stage- and size-based Lefkovitch-matrix population model (LEFKOVITCH, 1965; CROUSE *et al.*, 1987; CASWELL, 1989) and a dynamic-behavioral model (MANGEL and CLARK, 1988) to explore joint effects on population growth of predation on juvenile anchovy and schooled feeding on patchy prey by juvenile anchovy.

The chief functions of the stage- and size-based Lefkovitch model in this context are to simplify the report of results to a single value (i.e. the instantaneous projection of change in anchovy population size) and to allow the comparison of the juvenile tropho- and predation risk-dynamics to other effects at other life stages. In sum, a Lefkovitch model can evaluate combinations of growth rates and mortality rates that predict stable, increasing or decreasing populations.

Although population models can describe the consequences of given growth and mortality rates, they rarely explicitly consider the behavioral dynamics that give rise to them. However, modeling approaches from behavioral ecology have successfully predicted and explained many dynamical aspects of foraging behavior in animals (see STEPHENS and KREBS, 1986; MANGEL and CLARK, 1988). Specific cases have involved trade-offs between growth rate and predation risk avoidance in fish (WERNER *et al.*, 1983; DILL and FRASER, 1984; POWER, 1984; METCALFE *et al.*, 1987; ABRAHAMS and DILL, 1989; FRASER and GILLIAM, 1992). Also, although less behavior-explicit in their assumptions, a series of individually-based bioenergetic models have been applied to fish to model population growth rates (KITCHELL *et al.*, 1977; KERR, 1982; ROFF, 1983; BOISCLAIR and LEGGETT, 1989, 1991). Here we consider a schooling fish searching for patchy food in a world of predatory birds in flocks, predatory marine mammals in herds, and predatory larger fish. Such a species is likely to have its growth rate affected by both its bioenergetics and its behavioral responses to predation risk.

The northern anchovy is particularly amenable to a multi-level modeling approach. Its biology has been extensively studied for several decades both in the ocean and in the lab so that the bioenergetics of swimming and feeding are known (BLAXTER and HUNTER, 1982; BUTLER, 1989; BOGGS, 1991). Descriptions of fish school sizes and feeding behavior are likewise well documented (BLAXTER and HUNTER, 1982). Patchiness of zooplankton, which are the anchovy's prime prey, has been measured directly (KOSLOW, 1981; STAR and MULLIN, 1981) and acoustically (SMITH *et al.*, 1989). Lastly, a population model of the northern anchovy exists (BUTLER *et al.*, 1993) with direct estimates of most parameters, so that first approximations of juvenile parameters with no previous estimates can be inferred.

Our primary goal is to produce models that mimic what is observed in natural populations, particularly in relation to growth rates of wild fish. However, "fitting" a model does not validate its assumptions. Therefore, a second goal of our exercise is to produce novel and field testable hypotheses. The first two sections describe the methods and results of the population and behavioral models. The intersection of the results are then considered, and we then consider behavior/population models' predictions with several hypothetical scenarios of global climate change. It is important to note the methodology we employ is applied to *E. mordax* because of our extensive experience with

this species, but the techniques can be modified and extended to studies of other commercially valuable fish species (e.g. MANGEL, 1994).

THE POPULATION MODEL

We consider the population model in two stages, methods and results. One can view the existing model (Table 1) as a template with which to interpret the behavioral model below in terms of the population response to the environment. Artificial constraints on such a model include the facts that the model is deterministic, the model includes no explicit response to population density, it is assumed that the modeled population has a stable age distribution, and, is stationary for the entire period of response to the changed parameters. The principal value of the model is that it assembles the average functional responses to the environment and yields an instantaneous trajectory of population change.

Methods

It is beyond the scope of this paper to review the general methods of population modeling. It is sufficient to say that we have adopted the stage-specific matrix modeling technique of CASWELL (1989). The method we have used for dividing the anchovy population into stages follows that of SMITH (1985) and BUTLER *et al.* (1993) (Table 1). The nine stages of the life cycle are evaluated in terms of the duration of each stage, the mortality rate estimated for that stage, and the maternity function, which is the daily average number of female eggs produced per female that survive the mid-point of the first time step. Instead of the Leslie matrix, in which the time steps are equal and only mortality and maternity values are considered, we use the Lefkovitch matrix, which allows variation in the duration of each stage. Thus, we construct a 9×9 matrix in which the first row is the stage specific daily maternity function and the diagonal contains two values, the probability of surviving the time step, and the joint probability of surviving the time step and progressing to the next stage. The basic approach (BUTLER *et al.*, 1993) we have used is to assemble the best available estimates of the mortality, growth and maternity rates of each stage of the anchovy life cycle from the literature (Table 1). Since some mortality rate estimates are missing for the late larvae and juvenile stages, these have been filled by a generalized size-specific mortality rate function (PETERSON and WROBLEWSKI, 1984). Lastly, the early juvenile mortality rate has been "tuned" to yield an equilibrium population.

We have chosen to model the influences on growth and mortality of the 60–85 mm late juvenile of the central subpopulation of the northern anchovy. The reasons we have chosen this stage are: (1) it is beyond the complex stage where differentiation and metamorphosis occur (about 35 mm); (2) the anchovy has not yet begun to spawn (usually after 85 mm); and (3) the individuals in a cohort, over an 80 day period, appear to triple in dry weight while only decreasing by about half in number, leading to a massive cohort biomass increase.

In a Lefkovitch matrix model, any life-stage can be separated and the mortality and duration parameters and the maternity function (if any) manipulated without regard to the other stage parameters. Following manipulation of the predation risk and growth effects in the behavior model (see below), the importance of these perturbations through their range can be then compared with parameter changes in other stages. Since the original set of

Table 1. Estimated and postulated life history characteristics for the central subpopulation of the Northern Anchovy (sources in parenthesis)

Category	Length (mm)	Maternity Rate (daily	Instant. Mortality Rate (daily)	Growth Rate (mm) day^{-1}	Duration (days)	Initial Age (days)	Initial Dry (k) Weight (g)	Initial number	Bottom up Population Control (examples)	Top down Population Control (examples)
Egg	nil	0	0.231[a,b]	nil	2.9[c]	0	3.00E − 05	3.50E + 15	Adult fecundity Yolk quantity and quality	Filtering Predators
Yolk-sac Larva	0–4	0	0.366[d]	0.5	3.6[c]	2.9	2.55E − 05	1.79E + 15	Yolk quantity and quality	Filtering and Biting Predators
Early Larva	4–10	0	0.286[d]	0.5	12[c]	6.5	2.00E − 05	4.80E + 14	Protists and crustacean nauplii	Biting Predators and Expatriation
Late Larva	10–35	0	0.0719[f] *	0.56	45[g]	18.5	5.00E − 04	1.55E + 13	Microcrustacea	Fish, Birds and Expatriation
Early Juvenile	35–60	0	0.027964[f]	0.4	62[g]	63.5	5.00E − 02	6.10E + 11	Microcrustacea and Diatoms	Fish, Birds, Mammals and Expatriation
Late Juvenile	60–85	0	0.0044[f]	0.31	80[g]	125.5	3.00E − 01	2.54E + 11	Copepods, Diatoms	Fish, Birds and Mammals
Pre-Recruit	85–110	10.5	0.0031[f]	0.087	287[h]	205.5	9.00E − 01	1.09E + 11	Copepods, Diatoms	Fish, Birds and Mammals
Early Adult	110–135	199.2	0.0021[i]	0.025	1000[h]	492.5	2.00E + 00	4.46E + 10	Copepods, Euphausiids, Diatoms	Fish, Birds and Mammals
Late Adult	135–160	448.4	0.0021[i]	0.02	1250[h]	1492.5	4.00E + 00	9.00E + 09	Copepods, Euphausiids, Diatoms	Fish, Birds and Mammals

[a] BINDMAN, 1985
[b] STAUFFER and PICQUELLE, 1981
[c] LO, 1986
[d] PETERMAN *et al.*, 1988
[e] METHOT and KRAMER, 1979
[f] PETERSON and WROBLEWSKI, 1984
[g] BUTLER, 1987; WALDRON *et al.*, 1989
[h] FIEDLER *et al.*, 1986
[i] HUNTER *et al.*, 1985
[j] METHOT, 1989
[k] SMITH, 1985
* Used to tune model to $\lambda = 1.000$ @ age 2

parameters (Table 1) yield a population with no change (the innate rate of population increase r is 0, or λ is 1), the result of any perturbation in parameters is represented in the instantaneous rate of population change because all other parameters are not changed.

The method chosen to examine the parameter space for use in the behavioral model below is to substitute daily instantaneous mortality rates (imr) and duration parameters from the succeeding and following life stages. For each substitution, we will report the nominal population gain, λ, and report the change in the opposite parameter required to restore stability in population growth rate. We propose, for a first approximation that the ranges of imr and stage durations thus obtained will provide sufficient latitude for the behavioral model but constrain the examination of alternatives to the most likely segment of both parameter spaces.

Results

Within the anchovy late-juvenile stage, modeled as lasting 80 days, the individual juveniles grow in length from 60 to 85 mm, and in dry weight from 0.3 to 0.9 g. The number of individuals declines from 2.54×10^{11} to 1.09×10^{11}. Thus the cohort has gained 2.19×10^{10} g and has approached the maximum cohort biomass before the onset of maturation. Any combination of growth rate other than 0.31 mm day^{-1} or a daily imr other than 0.0044 that would achieve the same biomass would theoretically sustain the population. Any decline in the imr or decline in the duration of the stage would contribute to the growth of the population, all other parameters in other stages being equal.

Mortality rate. Consider the possibility that the mortality rate of the late-juvenile stage continued from the early-juvenile stage as 0.028 rather than 0.0044. With the stability conditions of growth rate of 0.31 mm day^{-1}, the probability of surviving to the next day is 0.9852 and the joint probability of surviving and advancing to the next stage is 0.0104. The probability of surviving the day under the higher mortality is 0.9691, and the joint probability of surviving the day and advancing to the next stage is 0.0033. The daily population growth rate would be 0.9985, leading to a population of 32% of the original over a 2 year period. For growth to overcome the influence of imr sustained from the early-juvenile period, the 80 day duration of the stage would have to be reduced to 12.57 days, with a daily probability of survival of 0.9069 and a joint probability of survival and advancement to the next stage of 0.0654. For 25 mm of growth to be accomplished the late juvenile would have to grow at a rate of 1.99 mm day^{-1}.

Consider the early achievement of a pre-recruit imr of 0.0031 in the late-juvenile stage rather than 0.0044. The probability of surviving the day under the pre-recruit imr is 0.9859 and the joint probability of surviving the day and advancing to the next stage is 0.0110. The daily population growth rate would be 1.0001, leading to a population 110% of the original over a 2 year period. To still have a stable population with an imr equal to the pre-recruit period, the 80 day duration of the stage would have to increase to 113.55 days, with a daily probability of survival of 0.9896 and a joint probability of survival and advancement to the next stage of 0.0073. Thus for 25 mm of growth to be accomplished the late juvenile would only need to grow at a rate of 0.22 mm day^{-1}.

Stage duration. Consider now that the duration of the late-juvenile stage has been lengthened by slow growth to that of the pre-recruit stage. Rather than taking 80 days the

stage is completed in 287 days. The probability of surviving the day is 0.9939 and the joint probability of surviving the day and advancing to the next stage is 0.0017. The daily population growth rate would be 0.9992, leading to a population 54% of the original over a 2 year period. The imr for an equilibrium population growth would have to be lowered to 0.00123 from 0.0044 with a daily probability of survival of 0.9959 and a joint probability of survival and advancement to the next stage of 0.0029. For 25 mm of growth to be accomplished the late juvenile could grow at a rate of 0.087 mm day^{-1}.

Lastly consider that the duration of the late-juvenile stage has been shortened by rapid growth to that of the early-juvenile stage. Rather than taking 80 days the stage is completed in 62 days. The probability of surviving the day is 0.9816, and the joint probability of surviving the day and advancing to the next stage is 0.0140. The daily population growth rate would be 1.0001, leading to a population 108% of the original over a 2 year period. The imr for an equilibrium population growth could increase to 0.00568 from 0.0044 with a daily probability of survival of 0.9809 and a joint probability of survival and advancement to the next stage of 0.0134. For 25 mm of growth to be accomplished, the late juvenile could grow at a rate of 0.40 mm day^{-1}.

Given the stage structure of this model, it would not be productive to examine instantaneous mortality rates outside the range of 0.028 and 0.00123, for those rates would exceed the rates indicated by exploring the range of durations of the adjacent stages. Similarly, durations outside the range of 13–287 days for completing the late juvenile stage would be excessive for this stage of research on the juvenile stage characteristics.

THE BEHAVIORAL MODEL

Methods

In its most basic description, the behavioral model is based on schools of anchovies swimming through the ocean and encountering patches of concentrated zooplankton. While swimming and feeding on the zooplankton, the anchovies themselves are vulnerable to predation. To predict their behavior we use the modeling technique of state-dependent optimization (MANGEL and CLARK, 1988; MANGEL and LUDWIG, 1992), with the key behavioral variable under the control of the fish being swim speed. Swimming rate affects many things, including: the metabolic cost per unit time, the rate of encounter with food patches, school shape, and the time spent in the zooplankton patches. Through these effects, swimming rate translates into a realized growth rate, which itself affects susceptibility to predators and eventually survival rate and reproductive success. A detailed description of the model is given in Appendix 1.

For reasons discussed above, we are primarily concerned with the late-juvenile life stage of *E. mordax* (from 60 to 85 mm in length). From the standpoint of mathematical tractability, this life stage is also easier to model because there is no need to have behavioral trade-offs between growth and reproduction. Juvenile anchovies only grow, they do not make eggs (HUNTER and GOLDBERG, 1980; HUNTER and LEONG, 1981; BUTLER *et al.*, 1993). We note, however, the size of a fish and reproductive ability have the potential to interact at later ages and affect juvenile foraging behavior. This is important in constructing a terminal fitness function for the model (see Appendix 1).

Zooplankton are defined here as a taxonomically heterogeneous assemblage of organisms of various lengths and biomasses. The assemblages can be composed of hundreds of

species, with individuals ranging in size from microscopic to several centimeters in length. For the purposes of the present work, productivity and patchiness are the most useful attributes to characterize. Unfortunately, standing crop and sample variance are the only attributes available. Standing crop at any instant reflects the difference of the temporal and spatial transport into and out of the local area, production, and consumption. Accurate estimates of these variables are difficult to obtain. Sample variance has many origins including the methodological variation among net tows, day–night differences, patterns of behavior, and hydrographic and physiological scales of each species (O'Connell, 1971; Smith, 1978). Although precise quantitative estimates are problematical, zooplankton consistently show a pattern of aggregation, rapid bursts of reproduction, followed by convergence and patch depletion by aggregations of predators, in addition to aggregation-destroying processes such as turbulent dispersal and mixing on several time and space scales (Smith *et al.*, 1989).

Zooplankton patchiness may affect the functional properties of search and feeding strategy in *E. mordax*. Most of the ocean volume has very low zooplankton density. For 35091 quantitative plankton tows in CalCOFI (California Cooperative Oceanic Fisheries Investigations) surveys, 40% of the zooplankters between 1 and 50 mm major dimension were found in 3.66% of the plankton tows. To approximate this situation, in our models we assume that large zooplankters ($\geq$1 mm in length) are found only in discrete patches, with only microplankton (phytoplankton and small zooplankton $<$1 mm) in the waters between the patches. Prey patches are defined as being cylindrical in shape, with an average radius of 634 m and the average distance between patches being 2553 m (Smith *et al.*, 1989).

Thus, in the behavioral model there are two habitats: prey patches containing large, abundant zooplankton, and the area between prey patches containing low-concentration microplankton. In nature, anchovies swimming in water without large, abundant prey will filter feed. However, if prey abundance increases, fish will shift feeding modes to biting at individual prey items (Leong and O'Connell, 1969; O'Connell, 1972). Therefore, we model the fish as bite-feeders in the prey patches and filter-feeders between patches.

Rather than modeling a complicated predator–prey interaction between the many species of zooplankters usually found within any given patch, we define three categories of patches as characterized by a single size class of zooplankton. These are: (1) large items (e.g. euphausids), where the zooplankters encountered by the fish are given a length of 4 mm, a biomass of 0.00763 g, and a swimming speed of 10 cm s^{-1}; (2) medium items (e.g. copepods), given a length of 1.8 mm, a biomass of 0.00455 g, and a swimming speed of 5 cm s^{-1}; (3) small items (e.g. amphipods), given a length of 1 mm, a biomass of 0.00256 g, and a swimming speed of 2 cm s^{-1} (the length and biomass estimates from Omori, 1969).

The effectiveness of bite-feeding by anchovies depends on the reaction distance of the fish to the prey. This, in turn, depends on the size of the fish (larger fish can see further), the size of the prey, the light level and the turbidity of the water. We have no estimates for the latter two factors in the anchovy–zooplankton system. However, several studies have estimated relationships between fish and prey size and reactive distance (Brawn, 1969; Ware, 1973; Werner and Hall, 1974; Confer and Blades, 1975; O'Brien *et al.*, 1976; Dunbrack and Dill, 1983; Dill and Fraser, 1984). From these studies we can derive a reactive distance (R) function based on the size of the anchovy and the zooplankter (see Appendix 2).

Many species eat anchovies. Instead of formulating a species by species functional response of predators to anchovies, we use two predation risk functions. One function

reflects the level of predation risk to anchovies based on the location of the fish school (i.e. is the school in a zooplankton patch?). We assume that fish inside a zooplankton patch are more at risk than outside of one. This assumption is likely to be valid for several reasons. First, school integrity tends to break down while in a patch, which makes fish more susceptible to predation (O'CONNELL, 1972;, SMITH, personal observation). Second, fish actively searching for prey are less able to remain vigilant for predators (MILINSKI and HELLER, 1978). Finally, predators are likely to be drawn to zooplankton patches because of increased detectability of the feeding fish. This may be particularly true for visual predators like sea birds or auditory hunters like dolphins, which may be able to home in on fish schools from many kilometers away because they are cognizant of others successfully feeding.

The second predation function assumes that as anchovies grow larger, they reduce their susceptibility to some predators (e.g. smaller piscivores). We model this decrease in risk by using an exponential function: $e^{-\alpha(L-5)}$, where $-\alpha$ is a scaling constant for the effect of larger size and L is the length of the fish in cm. Combining the two predation risk functions results in an estimate of a daily instantaneous mortality rate of:

$$\text{imr} = 0.003\, e^{-\alpha(L-5)} * [p(m-1)+1], \tag{1}$$

where p equals the proportion of the day spent inside the zooplankton patch and m is a scalar for how much more risky the patch is than the surrounding ocean ($1 \leq m \leq 40$ in the model). Therefore, any fish in the late-juvenile stage that does not enter a zooplankton patch ($p = 0$), will have an imr that approximates that of the next older life stage (≈ 0.003, see Table 1).

Results

In sum, the behavioral model predicts that *E. mordax* trades-off growth rate to lessen predation risk: fish do not grow as fast as they possibly can. The predominant way in which exposure to predation is regulated (and growth rate and imr thereby affected) is to vary swimming velocity between patches. Slow swimming decreases patch encounter rates, but also decreases predation rates. Conversely, the model consistently predicts that under almost all conditions and for all fish lengths, schools should swim very rapidly in zooplankton patches. In fact, under most conditions the model predicts that fish swim close to the chosen maximum rate of just under 50 cm s^{-1} while in zooplankton patches (although this rate contains both a searching and forward-directional vector, such that the time in patch is not always minimized). The predicted high velocities probably result from the fish being very efficient in capturing zooplankton (see below). In total, some factors have major effects on growth and survival, others have moderate effects, and some have minor to no discernable effect.

(*A*) *Major effects.* (1) *Predation risk differential between zooplankton patches and their surrounding ocean.* If the predation rate is higher in the food patches than in the water between them, anchovy schools spend significantly less time in the food patches and show reduced growth rates (Fig. 1). The important factor seems to be that patches have a greater risk. The magnitude of this differential is of lesser importance: a 10-fold increase in risk (4–40) only slightly reduces the predicted growth rate. Clearly, if fitness is a function of both

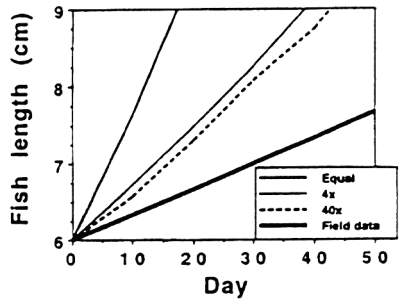


Fig. 1. Predicted growth rate of late-juvenile *Engraulis mordax* when zooplankton patches vary from being as risky as the water between them to being 40× more risky. The thick line is an estimated growth rate in the ocean (from BUTLER, 1989).

fish size (i.e. growth) and survivorship in achieving that size, then a pure net-energy maximization strategy is not optimal.

In Fig. 1 we also plot the observed mean length of late-juvenile *E. mordax* as it increased over the growing season in non-El Niño years (BUTLER, 1989). This gives an approximate estimate of growth rates in nature, although with the caution that the data do not represent the same fish, but rather different subsamples of a changing population. Samples taken later in the year were the survivors from earlier time periods, and thus may not represent all growth rates of all fish. Nevertheless, given this caveat, the predicted growth rates from the behavioral model exceed the observed, inferred rate. However, it is significant that when patches are assumed to be riskier places, the predicted growth rates are much closer to the field data than under the assumption that patches are equal in risk to their surrounding water. The latter assumption predicts fish should act as energy maximizers and it is hard to adjust the model with this assumption in such a way as to closely match the field data. Greatly increasing the cost of swimming or decreasing food availability still predicts fairly high growth rates (see below). Thus, the assumption of a more complex behavioral repertoire (i.e. response to both food and predation risk) seems an important factor to consider in *E. mordax* life history.

Finally, when patches are riskier than the surrounding ocean, schools spend less time searching within a patch per encounter. This means that the fish must be leaving the patch before reaching their stomach capacity. As such, this predicts that fish rarely totally fill their guts in habitats with plentiful zooplankton patches.

(2) *The type of predation risk.* Differential predation in and out of zooplankton patches is size-independent: the patches are always x-times more risky than the ocean for all lengths of *E. mordax*. However, the advantages of growing may be to reduce the number of predators capable of capturing an anchovy. When growth reduces overall predation risk rapidly (α in equation 1 is larger), feeding in zooplankton patches becomes much more advantageous and predicted growth rate increases (Fig. 2). The implication of this result is that population growth of *E. mordax* is dependent on changes not only in the absolute numbers of predators, but also in the predator community composition. Predators that act size-independently (or even prefer to attack larger fish), such as dolphins and sea birds (low α), will depress growth rates far more than size-dependent predators, such as small piscivores or larger conspecifics (high α). Predation on *E. mordax* schools mostly by size-

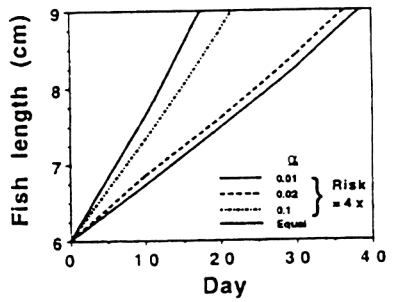


Fig. 2. Predicted growth rate of late-juvenile *E. mordax* when zooplankton patches are either as risky as the water between them or 4× more risky. The benefit of growing in terms of reduced predation risk is given for values of $\alpha = 0.01$ for the equal risk case and $0.01 \leq \alpha \leq 0.1$ for the 4× riskier case. Larger α values result in growth reducing predation risk at a more rapid rate.

dependent predators predicts that anchovies should behave more like net-energy maximizers.

(*B*) *Moderate effects.* (1) *Microplankton density between patches.* The density of microplankton between food patches has almost no effect on the predicted maximum rate of anchovy growth [Fig. 3(A)]. This is because fish in the model swim very rapidly between patches, resulting in an elongate school shape (BLAXTER and HUNTER, 1982) that increases the number of fishing seining the same water. In sum, bite-feeding in patches is energetically so much more profitable per unit time than filter-feeding between patches that the model predicts fish should minimize the time between patch encounters. Another result from the model also suggests that energy gained per unit effort from filter-feeding is low. In one variation of the model, we assume that it would cost anchovies more to swim with their mouths open as they filter feed. If this metabolic cost increases past 1.5 times that of normal swimming, filtering would be energetically non-profitable at swimming velocities predicted by the net-energy maximization version of the model. That is, fish expend more calories to filter than they collect.

Although microplankton density seems unimportant for a net-energy maximizing fish, it is much more important for a predation-risk sensitive fish [Fig. 3(B)]. A microplankton density increase of 4 or 10 times that of the normal mean density in the ocean ($=28$ mg m^{-3}: from BEERS and STEWART, 1967; O'CONNELL, 1971), predicts growth rates increase noticeably, although the predicted behavior of fish does not change (i.e. anchovies do not swim at different rate or change patch residence times). Swimming slowly between patches increases the pay-off of filtering because schools are wider and sweep a larger volume of ocean (BLAXTER and HUNTER, 1982). Besides seining microplankton, a filter-feeding fish also would collect fecal material and eggs from other fish in the school. Conceivably this would increase the pay-off for filter-feeding for schools of mature anchovies that are regularly spawning (mature *E. mordax* spawn every 7–10 days, HUNTER and MACEWICZ, 1980), but this is not the life stage of primary concern in this paper.

(2) *The energetic cost of swimming.* The cost of swimming in *E. mordax* has been measured to be proportional to velocity raised to a power of 1.44 (BOGGS, 1991; Appendix 2).

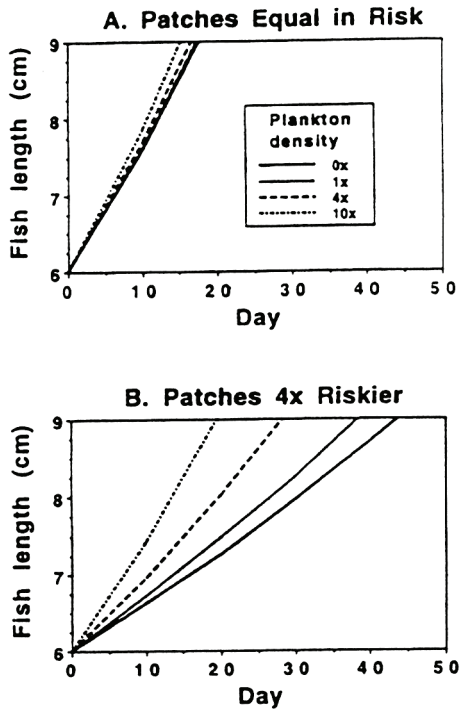


Fig. 3. The effect of microplankton density on fish growth. Predicted growth rate of late-juvenile *E. mordax* are given when zooplankton patches are either equal in risk to the surrounding water (A), or 4× riskier (B). The microzooplankton density in the water between patches is given a range of 0–10× the observed mean density of 28 mg m^{-3} in the waters of the California current.

Therefore, as fish swim their energy expenditures increase non-linearly. Raising the power to a higher estimate of 1.80 (Boggs, personal communication) results in the model having swimming costs that are four-fold greater at higher velocities (Fig. 4). However, such a potential increased cost is not translated into an equivalent reduction in predicted growth

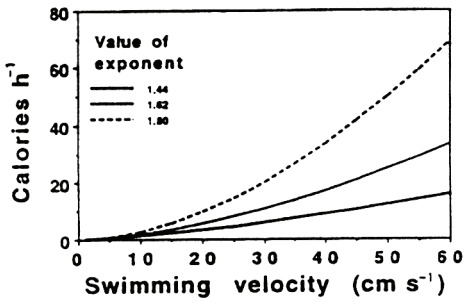


Fig. 4. The estimated cost of swimming for late-juvenile *E. mordax*. The costs are proportional to the velocity raised to a constant power. Boggs (1991) estimated this constant at 1.44. Higher estimates of 1.62 and 1.80 are given in comparison.

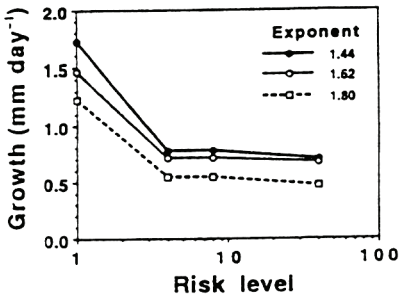


Fig. 5. Predicted growth rate for late-juvenile *E. mordax* with differing costs for swimming. Zooplankton patches range from being as risky as the water between them to being 40× more risky. The cost of swimming is proportional to the velocity raised to a power of 1.44 (from BOGGS, 1991, Appendix 2), or increased to higher levels of 1.62 and 1.80.

rates (Fig. 5). Where patches are assumed not to be differentially risky, there is less than a 50% reduction in maximum growth rates when costs rise proportional to 1.80. In the model, increasing the cost of swimming decreases the predicted velocity between patches from 24 cm s^{-1} with 1.44, to 17 cm s^{-1} with 1.62, and 14 cm s^{-1} with 1.80. Therefore, a combination of physiologically increased cost per unit effort and a behavioral reduction in swimming speed decreasing patch encounter rate accounts for the decline in maximum growth rate.

The model's predictions are less affected, however, by swimming costs when fish are predation-risk sensitive (Fig. 5). Because the fish are predicted to swim slowly between patches (on average, 4 cm s^{-1} with any exponential value), overall swim costs are not increased as much and there is no reduction in patch encounter rates.

In our model we assume that the fish swim in only one manner, which is more or less straight ahead. However, fish employ several types of swimming motions and behaviorally complex movements such as twisting and turning to capture prey may have almost 10 times higher net costs than pure straight-ahead swimming (BOISCLAIR and LEGGETT, 1989; BOISCLAIR and TANG, 1993). Although our model's predictions are unaffected by a wide range of costs for fish/zooplankter capture dynamics (see below), we may underestimate the difference in cost for active bite-feeding relative to filter-feeding. Overall, our cost estimates of swimming are not likely to be grossly in error as they are based on a 21-day growth experiment for *E. mordax* schools that likely reflected all types of swimming motions (BOGGS, 1991). If, however, being in a zooplankton patch has both increased predation risk and swim costs, anchovies may spend even less time in them than our model predicts.

(*C*) *Minor effects.* (1) *The dynamics of prey capture in the zooplankton patches.* The Gerritsen and Strickler (1977) model of predator–prey encounter rates requires estimation of several parameters, including prey velocity and escape behavior and reactive distances of predators (see Appendix 2). However, doubling the distance at which *E. mordax* can see a prey item, as well as assuming a 100% capture efficiency per strike, results in no appreciable change in the predictions. Likewise, decreasing prey capture efficiency results in fish devoting more time to search patches, but does not significantly reduce survivorship or growth rates. Including a term for the caloric cost of burst swimming (at 100 cm s^{-1}

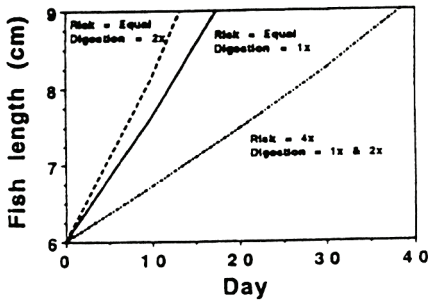


Fig. 6. The effect on predicted growth rates of late-juvenile *E. mordax* with a doubling of gut evacuation rate. The results are given for when the risk in the zooplankton patches is equal to the surrounding waters and when the risk is 4× greater. In the latter case, the predicted growth rate is identical with both evacuation rates

for 1 s) to capture prey item has no effect and can be omitted from future considerations.

(2) *The prey composition of zooplankton patches.* The physical characteristics of zooplankton, including factors like their length and swimming velocity, does not make much difference. In nature, growth rate is likely to be sensitive to the absolute density of zooplankton in a patch (i.e. biomass per unit volume of water: a variable not examined in this version of the model). However, the model suggests that zooplankter size in the range where bite-feeding is more efficient than filter-feeding (LEONG and O'CONNELL, 1969) would not, by itself, greatly influence anchovy behavior. The model assumes all zooplankton items are equally nutritious and digestible per unit biomass and time. As these factors may vary along with size across species (BOISCLAIR and LEGGETT, 1991; HEWETT *et al.*, 1991), species composition patches may have effects not addressed by this model.

(3) *Stomach capacity and gut evacuation rate.* The amount of food an anchovy can eat and rate of processing would seem to be important constraints for this model. However, they matter only under a scenario of net-energy maximization, where a doubling of the evacuation rate does increase predicted growth rates (Fig. 6). When the fish are reacting to predation risk, the doubling has no effect. The fish swim so slowly between patches that stomachs contain very little from the previous patch encounter with either evacuation rate. The fact that fish are predicted to leave patches with partially empty stomachs (see above) suggests that stomach capacity is also not an important constraining variable on their behavior.

COMPARISON OF POPULATION AND BEHAVIORAL MODELS

The results from the Lefkovitch population model and the behavioral model are not completely independent. Both use size-fecundity relationships for *E. mordax* (HUNTER and LEONG, 1981): to calculate population egg production in the Lefkovitch model, and to estimate a payoff function for growing and surviving through the late-juvenile stage in the behavioral model. The behavioral model uses the estimated mortality rate of the pre-recruit stage from the population model (Table 1) for the estimate of minimum daily

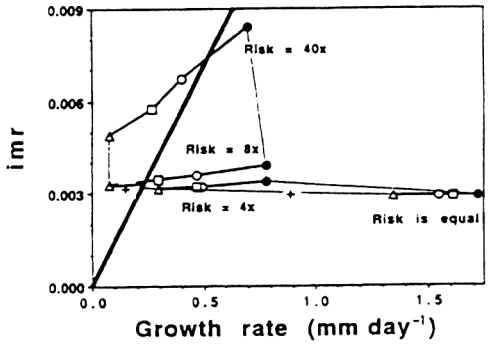


Fig. 7. Combinations of daily growth rate and instantaneous mortality rate (imr) predicted by the behavioral model. The solid circles represent the initial conditions where patches are separated by 2553 m and have a radius of 634 m. Results with climate change that increases the distance between patches by 50%, decreases patch volume by 50%, or both, are given by open circles, squares and triangles, respectively. Conditions under different environments, but with identical levels of risk in zooplankton patches are connected by thin, solid lines. The crosses are from a model scenario that includes added bioenergetic costs (see text). The thick line is from the population model and gives combinations of growth rates and imrs for late-juvenile *E. mordax* that can result in a stable population. Values to the left of the line result in declining populations and values to the right of the line can allow population increase.

instantaneous mortality rate for anchovies when not in zooplankton patches. Therefore, some congruence in predictions between the two models could be expected. However, the two models are independent in an important prediction. Both models produce paired values of imrs and growth rates. Although the imr should be similar, there is no *a priori* reason why predicted growth rates also should be similar.

In the population model, for each postulated growth rate from 0.1 to 1.75 mm day^{-1} we calculated the coincident imr which would restore the stationary population (see also BUTLER *et al.*, 1993). The result is a linear function of growth rate (Fig. 7, the heavy line). All values of imr to the right and below the balance mortality function will potentially allow population growth.

When growth rate–imr pairings are plotted for the results from the behavioral model, they are in accordance with the population model predictions (Fig. 7, solid circles). When risk in the zooplankton patches is low, the population is predicted to be increasing. When risk is very high (i.e. 40× greater) the population would still maintain itself. (Although the combination of imr and growth rate with a risk of 40× predicts an increasing population, this result is only for the late-juvenile stage. It may be that other life stages would require biologically unrealistic values to produce a stable Lefkovitch matrix—i.e. lower imrs for earlier stages or high growth rates for later stages). In sum, the behavior model based on known physiological and ecological data about anchovies predicts behaviors that produce growth rates sufficiently large enough to predict stable or increasing populations in a region of the ocean where anchovies do, in fact, survive. This seems an obvious point, but it is a necessary one. A model that predicts a crashing population when the real population is increasing must be seriously flawed.

Thus, a valuable result from this exercise is that two, quite different approaches to *E. mordax* behavior and population dynamics can produce convergent answers. As a first

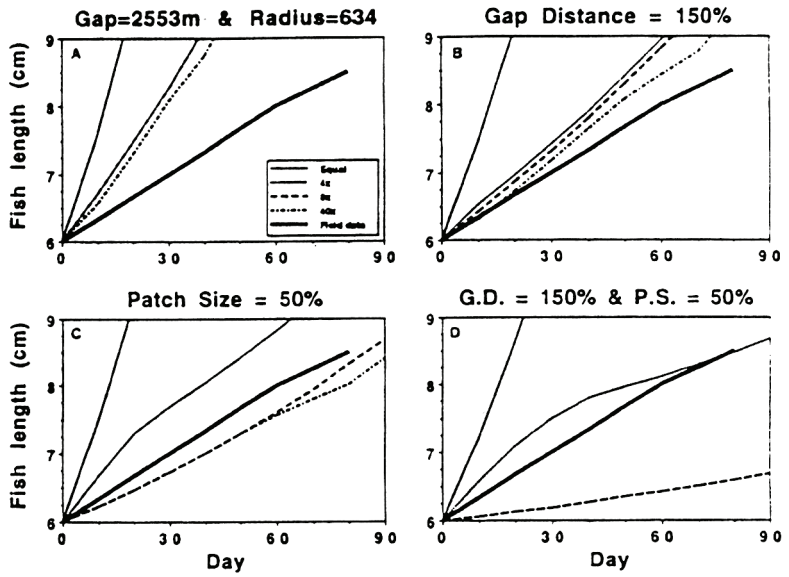


Fig. 8. Predicted growth rate of late-juvenile *E. mordax* in response to habitat decline. Zooplankton patches range from being equal in risk to their surrounding waters to being 40× more risky. For (A) the original conditions hold. For (B)–(D) distance between patches increases by 50%, patch volume decreases by 50%, or both. The thick line is the estimated growth rate in the ocean (from BUTLER, 1989). For all conditions α is 0.01.

approximation, this gives us confidence that we have begun to identify the key variables in the anchovy life cycle that strongly influence population-level changes.

SCENARIOS OF GLOBAL WARMING

It is clearly beyond the scope of this paper to predict precisely how global climate change alters the environment of foraging *E. mordax* schools. We assume, instead, that some changes are for the better and others are for the worse. It is conceivable that warming would improve conditions for anchovies and increase their numbers. Although such scenarios would be interesting to model, it is more practical to first consider possible negative effects. To that end, we model the behavioral response of schools to habitat decline in terms of availability of zooplankton patches.

We assume that potential consequences of climate change would be to increase the average distance between patches by 50%, decrease the average volume of a zooplankton patch by 50%, or both. The results suggest several possible consequences. First, if fish are assumed to maximize net energy intake (i.e. either ignore the added risk in patches or patches are not more risky), then the predicted growth rates are potentially large enough to maintain populations (Figs 7 and 8). If, however, patches are riskier places and anchovies are risk sensitive, then habitat decline has a major effect. Assuming that global warming does not increase the riskiness of patches, populations can still go from an increasing to a decreasing state (Fig. 7: points connected by thin, solid lines). For a given level of risk, the model predicts that imrs will be more stable than growth rates as the environment declines. The reduction in predicted growth rates is particularly evident in Fig. 8(A)–(D), where the differences between the theoretical maximum and fitness-

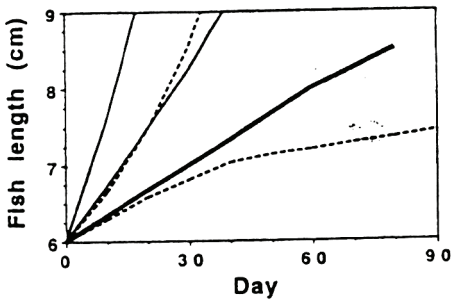


Fig. 9. Predicted growth rate of late-juvenile *E. mordax* in response to global warming. The dashed lines represent growth rates with increased costs for swimming, a doubled rate of stomach evacuation, and under conditions where patches are 50% further apart and 50% smaller. The solid lines represent the initial conditions. Risk in the zooplankton patch is either equal to the surrounding water (the leftmost thin lines) or 4× greater. The thick line is the estimated growth rate in the ocean (from BUTLER, 1989). For all conditions, α is 0.01.

maximizing rates are greatly increased with environmental decline. In several scenarios the predicted growth rates are less than the inferred present-day rates of late juveniles in the California current (BUTLER, 1989). Finally, if predators accumulate at zooplankton patches, predation risk could increase with habitat decline, thus further increasing the likelihood of a population decline.

Of course, when considering global warming, temperature effects on anchovy bioenergetics must be addressed. Temperature effects on fish can vary greatly across species, but more studies have found that metabolic rates increase with temperature (BRETT and HIGGS, 1970; EDWARDS, 1971; KITCHELL *et al.*, 1977; BEAMISH, 1990; HEWETT *et al.*, 1991). Therefore, in one last scenario of potential climate change, we assume an environment of 50% distance increase between patches and a 50% decrease in patch volume. We assume the warmer water increases the cost of swimming as a proportional power from 1.44 to 1.62. Finally, a potential benefit of warmer temperatures is that food is digested more rapidly (BRETT and HIGGS, 1970; EDWARDS, 1971; ELLIOT, 1972; JOBLING *et al.*, 1977). Therefore, we add to remaining scenario that gut evacuation rate is doubled.

The model assumes either no differential predation in the patches or a 4× greater risk. Under the former case, growth rate is lower, but not greatly so relative to the maximum growth rate with the initial set of assumptions (Fig. 9). However, growth in the latter case is substantially less than under present-day conditions. The combinations of imrs and growth rates for this climate change scenario are plotted as two crosses in Fig. 7. It seems that under this harsh scenario of climatic changes, anchovy populations could go into decline if the fish behave in ways that reduce predation risk at zooplankton patches, even if the predation risks are not that great.

DISCUSSION

In this paper, we attempt to unite three methodological approaches in behavioral ecology and population biology to model the foraging dynamics of *E. mordax* schools. First, we use a Lefkovitch matrix population model to explore ranges of the late-juvenile stage parameters that would be productive to investigate. In conjunction with this model, we add a bioenergetic model of an anchovy school moving and feeding in the California

current. The bioenergetic data are placed in the framework of a state-dependent, dynamic optimization model to predict the set of behaviors that maximize eventual reproductive output. The predicted growth rates and imrs from the behavioral model are compared to both the population model and field data for robustness of result.

Paramount is the finding that the effects of the trade-offs between predation risk and growth rate are substantial. Fish are not simply trying to maximize growth rate through finding as much food as possible. Rather, the model strongly suggests *E. mordax* schools trade-off growth for safety (also see MANGEL, 1994).

Previous bioenergetics models have been applied to several fish species in an attempt to explain observed growth patterns (KITCHELL *et al.*, 1977; KERR, 1982; ROFF, 1983; BOISCLAIR and LEGGETT, 1989). The models have had varying degrees of success (see discussion by HEWETT *et al.*, 1991; BOISCLAIR and LEGGETT, 1991), but all have the implicit assumption that fish are maximizing growth rates within any given environment. Whether this assumption is true may vary across species, but it is clearly not always true with fish. Juvenile bluegills prefer the habitat that maximizes growth only when predators are absent. In the presence of bass they choose to forage in safer, but food-poorer, habitats that increase survivorship at the expense of growth rate (WERNER *et al.*, 1983). Other examples of habitat use patterns that both reduce predation risk and growth rates have been observed in catfish (POWER, 1984) and poeciliads (FRASER and GILLIAM, 1992). Behaviorally, risk avoidance reducing foraging success has been shown in salmon (DILL and FRASER, 1984; METCALFE *et al.*, 1987), perch (HOLBROOK and SCHMITT, 1988) and guppies (ABRAHAMS and DILL, 1989).

Our behavioral model suggests that anchovies are similarly sacrificing growth for safety. It is possible that our measures and assumptions about energetic costs may have some errors associated with them, but it seems unlikely that they could be wrong to the degree and consistently in the direction required to lessen the predicted growth rates for pure, net-energy maximizing anchovies to the level of field estimates.

If anchovies are truly reducing predation risk as suggested by our behavioral model, then several novel and testable predictions follow. First, schools should swim slowly between zooplankton patches or possibly in a seemingly inefficient and undirected course of travel. Fish are predicted not to swim crisply from point to point. Second, once in a zooplankton patch, fish should swim extremely rapidly while biting at their prey. Third, schools should routinely leave extant zooplankton patches, with many if not most of the fish still having partially empty stomachs.

There are a number of interesting results from the behavioral model that are more difficult to test. The ocean waters outside of the dense zooplankton patches have been thought to contribute little by way of filter-feeding to the overall energy budget of *E. mordax* (LEONG and O'CONNELL, 1969; O'CONNELL, 1972). In an absolute sense, our results support this view: filter-feeding is much less cost efficient than bite-feeding, and changes in microplankton density have small effects on maximum theoretical growth rates. Nevertheless, if schools swim slowly between patches to reduce predation, then increases in filterable microplankton can substantially increase growth rates. This may help explain why clupeiod fish invest so much energy in filter-feeding apparatus and behavior (BLAXTER and HUNTER, 1982), when on the face of it, filter-feeding appears to provide such a small, relative energetic return.

The behavioral model also predicts that the composition of the predator guild is important. Avoidance of predators that indiscriminately attack fish of all sizes, or

preferentially attack larger fish, will depress growth rates more than avoidance of predators hindered by increasing anchovy size. Therefore, predicting future changes in the populations of *E. mordax* due to climate change also will require a consideration of how the same changes will affect the various predator species. For example, if climate change negatively affects dolphin and sea bird numbers, in fact it may increase anchovy growth rates and thus possibly increase population size.

It is also clear that if anchovy behavior is more complex than simple net-energy intake maximization then extrapolating habitat change to future fish populations may be troublesome. Our results suggest that habitat decline generally exaggerates the effects of predator avoidance. Whether populations of fish can survive climate change will require understanding more than whether or not areas have enough prey to support an anchovy population. Sustainable or commercial populations of *E. mordax* may be limited as much, or more so, by predators than by prey availability.

The models we have presented are not intended to be complete. We assumed a constant patch size and distribution, and a constant school size. Both of these are quite variable in the field (BLAXTER and HUNTER, 1982; SMITH *et al.*, 1989) and to adequately understand and predict *E. mordax* population dynamics will require examining the effects of variability in all these parameters. For example, in a simulation of the early larvae stage of anchovies, food patchiness altered growth rate (VLYMEN, 1977). The maximum growth rate was at a food patchiness intensity of $k = 0.17$, with growth rate dropping sharply with more dispersed food and dropping slowly with more aggregated food. A similar relationship may exist for populations of juvenile anchovy. Likewise, there must be an optimal school size that balances predation risk and foraging gain. Very small schools or individual fish seem to rapidly fall prey to predators and very large schools must suffer reduced food intake per fish. How groups form, coalesce, and break apart is a process yet to be modeled for *E. mordax*.

In summary, the results presented here are a promising beginning. Long term success in this project will hinge upon the incorporation of other important parameters and the testing of the predictions generated against field data and the behavior of fish in the wild.

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APPENDIX 1: DESCRIPTION OF THE BEHAVIORAL MODEL

We use the techniques of dynamic optimization (MANGEL and CLARK, 1988) to model a situation where a school of anchovies swim through an ocean environment of high density food patches of zooplankton (euphausids, copepods, and amphipods), with only low densities of microplankton (small zooplankton and phytoplankton) between patches. The fish choose how fast they swim through the open ocean when not filter-feeding, how much time they spend searching for food in the zooplankton patch, and how fast they swim through the zooplankton patch when not searching.

Although our interest is in the late-juvenile stage, to understand behavior of fish in that stage we need to specify a terminal function for fitness for fish surviving that stage. Therefore, a second dynamic optimization model was constructed for the trade-off of growth for egg-production for mature anchovies (based on a size:fecundity relationship from HUNTER and LEONG, 1981). Fitness is defined as the combination of resources devoted to egg production (non-linearly increasing with fish size) and survivorship to egg-producing size (also non-linearly increasing with growth) that maximizes total egg production over a 90-day season. A robust result across many assumptions of growth-egg-production trade-offs is that fitness is linearly related to fish size (Bouskila and Nonacs, unpublished data). The output from this model of the egg-producing adult stage of life is the terminal fitness function for the late-juvenile stage model discussed in this paper. (See Appendix 2 for the fitness function used and all other physiological and mathematical relationships used in the model.)

In the model, we have a size range of fish from 5 to 14.98 cm, using a step size of 0.02 cm. This far exceeds the size range of late juveniles so as to eliminate "edge" effects from the model (i.e. if a fish is constrained such that it cannot grow larger than 8.5 cm, then as it approaches that size its predicted behavior will be severely affected).

In a series of nested loops, we calculate the fitnesses for all possible combinations of swimming velocities between and within zooplankton patches. Between patch velocities are given an integer range of 1–60 cm s^{-1}. A zooplankton patch is assumed to occupy a cylindrical volume with a depth of 10 m, with an average surface area estimate of a radius of 634 m (SMITH *et al.*, 1989). A fish school upon encountering a zooplankton patch expands to fill the entire volume with an equal number of fish m^{-3} and, after feeding, contracts to its original size and exits the patch in a randomly chosen direction. Therefore, the average distance a fish from a school travels in entering and exiting a patch is equal to twice the average chord length of the circular surface area of the patch, which is 2.401 times the radius of the patch. This is the minimum distance a fish swims in a food patch if it swims only in straight lines. However, it is likely that a fish's movement will have both a forward component (to move through the patch) and a lateral movement component (to search for prey). The true velocity of the fish in the patch is a function of both: $v_p = (v_f^2 + v_s^2)^{0.5}$. The model allows fish to choose integer values of v_f and v_s, subject to the constraint that $v_p \leq 50$ cm s^{-1}. Combinations of two components can result in schools spending most of their time in food patch traveling ($v_f \gg v_s$) or searching for zooplankton ($v_f \ll v_s$).

Time in the food patch is calculated as a function of the patch radius divided by v_f. The available prey items in the patch per fish in the school is calculated as a function of patch size, zooplankter density, and number of fish in the school (which is a function of fish length because absolute school volume is fixed to be 9000 m^3; see Appendix 2). The maximum number of zooplankters a fish can potentially eat is calculated as a function of its stomach capacity and the amount of food remaining from its previous patch encounter. The number of zooplankters actually encountered in the time allocated to searching the patch is given from a predator-prey encounter model by GERRITSEN and STRICKLER (1977), with the added constraint of a 50% capture efficiency and a 1 s handling time. The number of zooplankters consumed is whichever of the above three values is the least.

All zooplankton densities are calculated as individuals m^{-3} by the relationship of $0.014/w * e^{3.6}$ from SMITH *et al.* (1989) which is the mean measured overall density of zooplankton. The correction factor of 0.014 reflects that zooplankton densities were initially measured as g 1000 m^{-3} over 140 m (rather than the depth of 10 m we use for our model) and w is the biomass estimates for a given type of zooplankter. The water between patches is assumed to have low densities of microplankton (28 mg m^{-3}); a situation that favors filter-feeding in *E. mordax* (LEONG and O'CONNELL, 1969; O'CONNELL, 1972).

Because anchovies travel in large schools, individual fish will be seining the same water as others. The degree of overlap will depend on the number of fish front to back in the direction of forward motion of the school. BLAXTER and HUNTER (1982) noted that anchovy schools become more elongate in the direction of travel as swimming velocity increases. Therefore, the faster the school swims, the more fish will be in a row seining the same water. The frontal area of a volume of water seined by a filter-feeding fish is assumed to be proportional to 1/10 the fish's length, such that area = π (length/10)^2. About $\frac{1}{4}$ of the fish in a moving school are filter feeding at any given moment and fish swim at $\approx$10 cm s^{-1} while filtering (Smith, personal observation). Thus, for any distance swum in the open ocean, the model estimates how much microplankton is taken per fish depending only on the density of the microplankton and the anchovies swimming velocity.

A foraging "day" has 12/12 hours of light and dark. During the daylight hours fish are swimming in the open ocean and in zooplankton patches as described above. At night, fish are assumed to be relatively stationary and swimming at 3 cm s^{-1}. The school is allowed to expand to 3× its daylight volume. Anchovies filter-feed at night (Smith, personal observation) and therefore the model assumes that during the night the school seines 100% of the microplankton contained within its volume (each fish is assumed to have equal seining success).

For anchovies about 35% of the calories contained in their food are not assimilated (BOGGS, 1991). Therefore, from the remaining 65%, the metabolic costs of maintenance and swimming must be paid, with the excess being allocated to growth. The model simulates growth by transposing excess calories into biomass increase from HUNTER and LEONG's (1981) calculated relationship of the caloric content of various tissues in *E. mordax* (given 15% body fat in juvenile fish: Smith, personal observation). Any excess calories collected by a foraging fish are added to its existing caloric biomass and then back-calculated into a new length. If a fish does not collect enough calories to maintain its present length, it is given a zero survivorship. Otherwise, survivorship is calculated as a function of the fish's current size and the proportion of time it spends in zooplankton patches. This value is then multiplied by the fitness function for the fish's new length. The combination of swimming velocities resulting in the highest fitness value is therefore the fish's predicted behavior. Growth and survivorship are measured over 10-day periods, and the model is back-iterated over a 90 day period according to the dynamic optimization methodology (see MANGEL and CLARK, 1988).

APPENDIX 2: PHYSIOLOGICAL AND MATHEMATICAL RELATIONSHIPS

Caloric expenditures in *E. Mordax* (from BOGGS, 1991):

Swimming metabolism = $0.00094L^{2.14} * v^{1.44}$ calories per hour (where v is swimming velocity in cm s^{-1}, and L is length in cm).

Basal metabolism = $0.4683L^{2.4}$ calories per day.

Caloric content of a fish L cm in length (from HUNTER and LEONG, 1981):

$6.151L^{3.195}$ calories.

Stomach capacity (in g) for an anchovy (from LEONG and O'CONNELL, 1969):

$0.0933M + 0.0531$, where M is fish biomass in grams (from COLLINS, 1969; $M = 0.0099L^{3.009}$).

Stomach emptying rate (from BOGGS, 1991):

$e^{-0.106t}$ where t is the time (h) since the food was ingested.

Anchovy–zooplankter encounter rate (modified from GERRITSEN and STRICKLER, 1977):

$Z = 1 + 2/\{(\pi R^2 d/3) * [(u^2 + 3v_p^2)/v_p]\}$ seconds, where R is the reactive distance of the fish, d is the density of zooplankton per m^3, and u and v_p are the swimming velocities of the zooplankton and fish, respectively ($v_p > u$). The model assumes a 50% successful capture rate per encounter due to either the prey escaping or interference with other fish in the school, plus a 1 s handling time per prey. The energetic cost of capturing a prey item is calculated as the cost of swimming at a velocity that captures a prey item swimming directly away from an approaching anchovy one second after it enters the fish's reactive distance. R is best estimated from numerous studies on other species (BRAWN, 1969; WARE, 1973; WERNER and HALL, 1974; CONFER and BLADES, 1975; O'BRIEN *et al.*, 1976; DUNBRACK and DILL, 1983; DILL and FRASER, 1984), as equal to $13.4sL$, where s and L are the lengths (in cm) of the prey item and the anchovy.

Frontal area of school swimming at velocity, v (from BLAXTER and HUNTER, 1982):

$25.3A^{0.5} * v^{-0.42}$ m^2, where A is the surface area of the school (for the purposes of this model we use an average surface area of 900 m^2, with a mean depth of 10 m per school).

Number of fish in a school (from GRAVES, 1977):

Anchovies have been observed to swim separated by average of 1.2 body lengths. Therefore, we divide the given school volume of 9000 m^3 by 2.2 × 1.2 × 1.2 × fish length^3 (in m).

Terminal fitness function from second dynamic optimization model:

Size-specific fitness = 14313 + 5389 * length (cm).